THE ENIGMATIC ARTHROPOD *DUSLIA* FROM THE ORDOVICIAN OF CZECHOSLOVAKIA

by IVO CHLUPÁČ

ABSTRACT. A restudy of *Duslia insignis* Jahn, 1893 from the Upper Ordovician of the Barrandian area, Bohemia, indicates that this trilobate arthropod, originally referred to polyplacophorans, cannot be assigned to true trilobites but shows some morphological analogies with *Cheloniellon*, *Pseudarthron*, and *Triopus*. *Duslia* inhabited a nearshore shallow marine environment and was probably a benthic animal which lived buried in sandy substrate near the sediment-water interface.

THE Upper Ordovician Letná Formation of the Barrandian area, central Bohemia, has yielded, apart from trilobites and other fossils, some remarkable remains of unusual arthropods; these were partly described by Barrande (1872) and later tentatively assigned to the aglaspids, xiphosurids, and eurypterids (Chlupáč 1965; discussion in Bergström 1968; Eldredge 1974). One member of this group of enigmatic arthropods is *Duslia insignis*, originally described by Jahn (1893) as a chitonid mollusc. It was recognized as an arthropod by Pilsbry (1900) and Fritsch (1908), although Knorre (1925) still assigned it to the polyplacophorans. After the exclusion of *Duslia* from the polyplacophorans by Pompeckj (1912) and Quenstedt (1932*a*, *b*), it was referred with some doubt to the burlingiid trilobites (letter of A. Liebus cited by Quenstedt 1932*b*; Broili 1933) and later to the cheloniellid arthropods (Chlupáč 1965), being definitely rejected from polyplacophorans by Smith and Hoare (1987). *Duslia* was omitted from the *Treatise on Invertebrate Paleontology* and the present revision, based on new and previously unstudied material, is the first since its original establishment in 1893.

The new reference material includes collections made at Veselá, near Beroun, at the turn of the century and recently by Dr M. Šnajdr and the author; all are deposited in the National Museum, Prague (L) and in the Geological Survey, Prague (ICh).

SYSTEMATIC PALAEONTOLOGY

ARTHROPODA

Genus DUSLIA Jahn, 1893

Type and only known species. Duslia insignis Jahn, 1893, from the Upper Ordovician, Barrandian area, Czechoslovakia.

Diagnosis. Trilobed and dorsoventrally flattened, thin exoskeleton of oval outline, with conspicuous spinose fringe. Cephalic region large, with distinctly differentiated conical glabellar area and smooth genal areas lacking eyes. A continuous fringe composed of flat spines borders the entire cephalon, including the posterolateral margin. Trunk composed of ten tergites with clearly defined rhachis and flat pleurae; pleural furrows shallow. Pleurae arranged radially; first two expand anterolaterally, third laterally, the more posterior posterolaterally. Abaxial extremities of pleurae bordered by spines continuing on the posterior pleural margins. Trunk terminated by short telson and spinose furcal rami of medium length. Other appendages unknown.

Occurrence. Duslia occurs sporadically on the north-west slope of Ostrý hill near Beroun, and at Vaselá in the gorge and on the ridge north-west of the former Veselá farm. At the latter locality, *Duslia* is concentrated

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in greater abundance in a distinct layer. Both localities belong to the fossiliferous biohorizon within the upper part of the Letná Formation (Chlupáč 1965).

Duslia insignis Jahn, 1893

Plates 56 and 57; text-fig. 1

1893 *Duslia insignis* Jahn, pp. 592–599, pl. 1, figs. 1–3.
1900 *Duslia insignis* Jahn; Pilsbry, p. 434.
1908 *Duslia*; Fritsch, p. 9.
1912 *Duslia insignis* Jahn; Pompeckj, p. 357.
1925 *Duslia insignis* Jahn; Knorre, pp. 497–499, text-fig. 1.
1932*a* *Duslia insignis* Jahn; Quenstedt, p. 555.
1932*b* *Duslia insignis* Jahn; Quenstedt, p. 86.
1933 *Duslia insignis* Jahn; Broili, pp. 30–31.
1960 *Duslia insignis* Jahn; Smith, p. 174.
1965 *Duslia insignis* Jahn; Chlupáč, p. 31.
1987 *Duslia insignis* Jahn; Smith and Hoare, p. 34.

Type material. Holotype (by monotypy), L26148, an internal mould (original of Jahn 1893, pl. 1, fig. 1; refigured here as Pl. 56, fig. 2), from Ostrý hill (north-west slope), near Beroun, central Bohemia, Czechoslovakia. Upper part of Letná Formation (oldest fossiliferous horizon with *Deanaspis goldfussi* (Barrande) distinguished by Chlupáč 1965); Lower Berounian (late Llandeilian or early Caradocian).

Other material. L27106 from the type locality. All other material from Veselá: five slabs (L26149, L26150, L26157, L26160, ICh522) each bearing two specimens (designated *a* and *b*); twelve other specimens (L26151–26156, L26158, L26159, L26161, L27105, ICh521, ICh7003), preserved as internal moulds and counterparts in impure sandstones or quartzites.

Description. Dorsal exoskeleton broadly oval in outline, length/width ratio 1·1–1·3. Cephalic region large and flat, subsemicircular in outline. Subconical, posteromedially placed and gently convex glabellar area is markedly delimited by broad and laterally pit-like, deepened but indistinct furrows. Transverse lobation less distinct; apart from the incompletely differentiated occipital ring, two or three anterior lobes are slightly indicated in some specimens (L26151, L26155, L26161) by shallow transverse furrows. Entire glabellar region depressed, and convexity of glabella does not exceed that of lateral parts of cephalic shield. Preglabellar and genal regions smooth, without any traces of eyes. Indistinct shallow depressions (usually two) radiate from glabellar region anterolaterally in some specimens (holotype L26148; best in L26150), suggesting differences of convexity in genal regions. Narrow, shallow, rather sharp furrow, running parallel to posterior margin and fading before reaching lateral cephalic margin, delimits the posterior border. Entire outer margin of cephalic shield bears marked fringe of closely spaced, flat spines of almost equal length, becoming only very slightly longer towards the genal angles. Fringe sharply separated from flat surface of cephalic shield by continuous furrow which in some specimens shows gentle increase of anterior convexity frontomedially (Pl. 56, figs. 1, 2, 4, 5; Pl. 57, fig. 2). Spines arranged radially and, as shown by L26161 (Pl. 57, fig. 2), they continue along posterolateral angles of cephalic shield up to posterior border, shortening markedly adaxially. Flat anterior doublure, gently broadened medially, is shown by L26160*b*.

On the trunk, ten tergites with clearly differentiated rhachis are defined by narrow and shallow lines which continue from rhachis without interruption onto the lateral pleural regions; these lines evidently represent intertergite boundaries. Rhachis composed of gently convex anteriorly curved rings and depressed, sagittally

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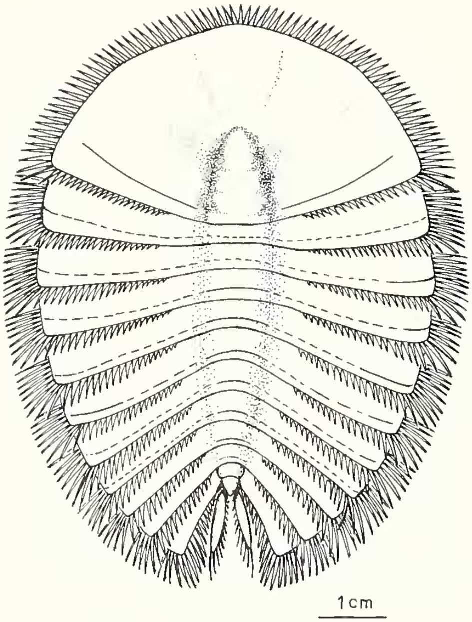
EXPLANATION OF PLATE 56

Figs. 1–5. *Duslia insignis* Jahn, 1893. Letná Formation, Upper Ordovician; Veselá (figs. 1, 3–5), Ostrý (fig. 2), Bohemia, Czechoslovakia. 1, L26158, internal mould, ×0·8. 2, L26148, holotype, internal mould with partly exposed doublures of left pleurae, ×0·8. 3, L26160*a*, internal mould, less deformed, ×1·1. 4, L26156, incomplete cephalic shield and anterior pleurae with spinose fringe, ×0·9. 5, L26151, internal mould, slightly bent laterally, ×0·8.

CHLUPÁČ, *Duslia*



TEXT-FIG. 1. *Duslia insignis* Jahn, 1893. Reconstruction of dorsal exoskeleton.

shorter articulating facets. Rather broad and deep depressions separate the rhachis from markedly transversely broader pleural regions.

Pleurae arranged radially; the two anterior expand anterolaterally, the third laterally, and subsequent ones posterolaterally with successively diminishing angle of divergence. Pleurae widen slightly abaxially and bear shallow and indistinct pleural furrows that subdivide anterior pleurae into unequal bands; posterior bands usually more convex and narrower than anterior bands (best shown by L26160*a*, Pl. 56, fig. 3). Details of convexity of individual pleural parts generally obscured by overlapping and flattening of tergites. Abaxial extremities of pleurae bordered by closely spaced spines which lengthen slightly towards posterolateral angles, along which the spines continue up to posterior pleural margins, partly overlapping subsequent pleura. The spines represent extensions of pleural margins and, although in shape and arrangement they resemble trilobite appendages, they evidently belong to the dorsal exoskeleton as distal extremities of pleurae. Details of spines generally obscured by coarse-grained sediment; they are clearly evident in L26151 (Pl. 56, fig. 5; Pl. 57, fig. 1), L26152, L26154, L26158, ICh521, and L26160*a* (Pl. 56, fig. 3; Pl. 57, fig. 4). These specimens show differences in length of individual spines, the longest and strongest being at posterolateral pleural tips.

In specimens with partly exfoliated outer surface, flat pleural doublures are seen (L26153; Pl. 57, fig. 3; also L26160*b*).

Convexity of pleural regions generally low, but exceeds that of rhachis—in transverse section, rhachis lies in broad depression (Jahn 1893, pl. 1, fig. 3). Spinose fringe gently upraised in some specimens (e.g. L26158, L26161). Although these features might have been accentuated by compaction, the lack of deformation suggests their primary nature.

Posterior termination of trunk usually inadequately preserved in the coarse-grained sediment. L26160*a*,

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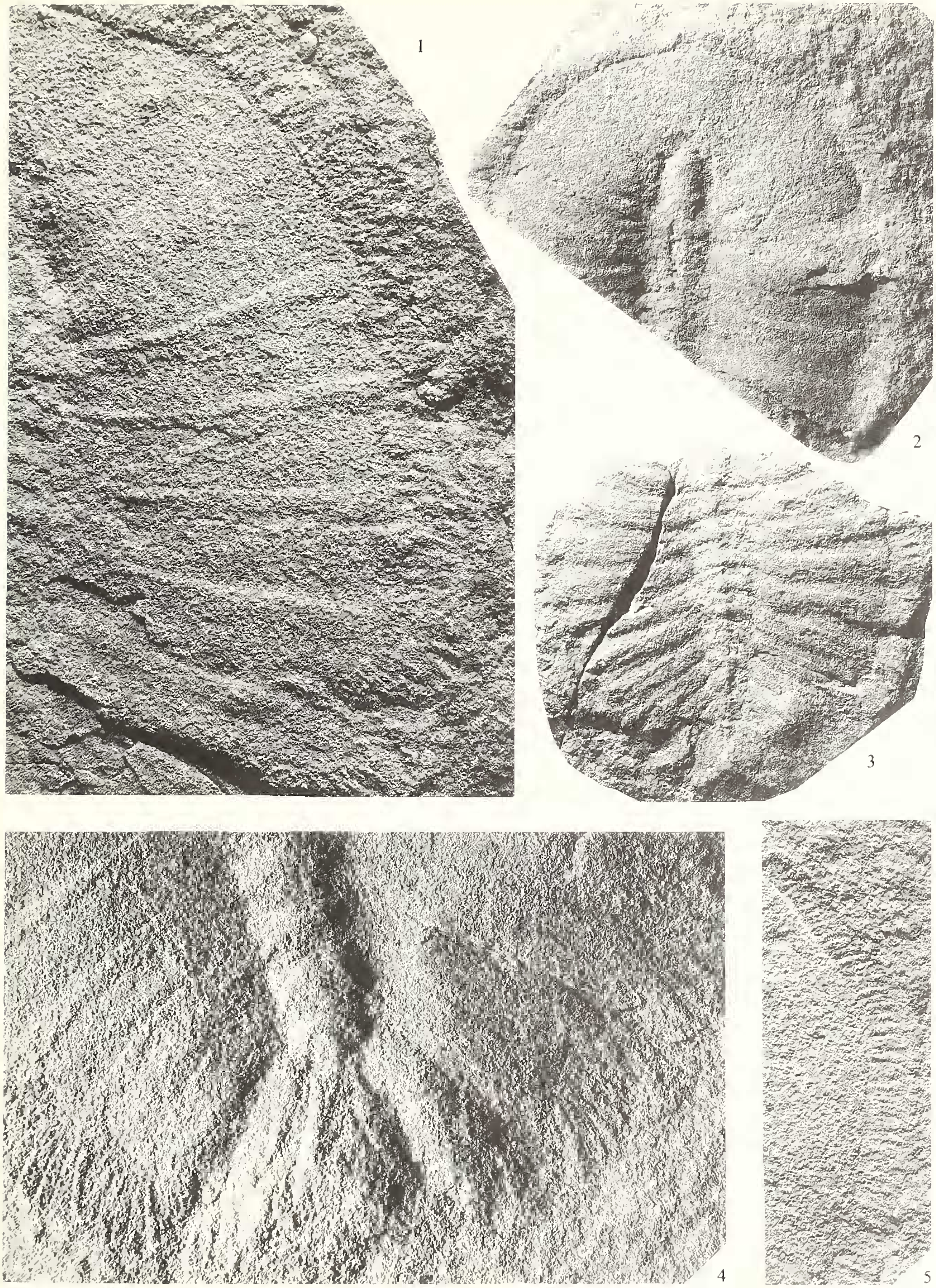
EXPLANATION OF PLATE 57

Figs. 1–5. *Duslia insignis* Jahn, 1893. Letná Formation, Upper Ordovician; Veselá, Bohemia, Czechoslovakia. All internal moulds. 1, L26151, enlarged part showing spinose fringe continuing along the posterolateral extremities of pleurae, ×1·5. 2, L26161, specimen showing spinose fringe continuing along the posterolateral angle of cephalic shield, surface slightly weathered, ×1·3. 3, L26153, damaged trunk with partly exposed doublures, ×1·0. 4, L26160*a*, enlarged posterior part of the trunk with telson and furcal rami, ×2·3. 5, L26156, enlarged spinose cephalic fringe, ×1·5.



CHLUPÁČ, *Duslia*

whose relief is most distinct, exhibits behind last rhachial ring a suboval and posteriorly narrowed plate—probably a telson—to which are attached (articulated?) two prolonged lanceolate lamellae, interpreted as furcal rami (Pl. 57, fig. 4). These are somewhat narrower and more convex than the last pleurae and bear spines analogous to those of pleurae (indicated in L26153, L26160*a*, L26149*a*—here markedly convex furcal rami).

Holotype has (slightly extrapolated) length of 86 mm and maximum width of 75 mm (including fringe). Other specimens are 85–110 mm long, 75–95 mm wide (extrapolated, including fringe). Largest incomplete specimen (ICh521) suggests length of *c*.120 mm.

Discussion. All the known specimens of *Duslia* are articulated and, if not broken after removal from the rock, they are preserved as complete dorsal exoskeletons. This suggests a rather tight connection between individual elements of the exoskeleton, especially in the rhachial region. As shown by the dorsoventrally flexed specimen ICh7003, the pleurae could have been removed up to the rhachial furrows. Other specimens (e.g. holotype L26148, Pl. 56, fig. 2; L26151, Pl. 56, fig. 5) show gently detached pleurae in abaxial parts of the posterior segments. The rather firm connection in the rhachial region seems to be a characteristic feature of *Duslia*, and contrasts with trilobites.

The carapace is markedly thinner than in the associated trilobites; the trilobite remains generally show no marked deformations and are preserved in limonite (which replaces the calcium carbonate of unweathered Letná Formation). In contrast, the remains of *Duslia* lack a thicker limonite cover and are preserved in a similar manner to the associated conulariids and other thin-shelled fossils with an originally phosphatic shell. Although the cuticle of *Duslia* has been completely dissolved, this mode of preservation may reflect a different original composition of the carapace to that of trilobites.

Some specimens show exoskeletal parts that are gently deflexed in a horizontal plane; the holotype (L26148) is slightly curved to the right in the posterior part of the trunk (Pl. 56, fig. 2), L26151 is gently bent laterally (Pl. 56, fig. 5), and similar patterns are shown to a lesser degree by some other individuals. Some flexibility should therefore be considered likely.

The thin carapace of *Duslia* was commonly affected by compaction which resulted, for example, in a gently differing convexity of the rhachis—although the general flatness of the entire exoskeleton remains characteristic. Asymmetrical irregularities are in most cases caused by coarser rock grains, fossil partings, or ichnofossils beneath the thin carapace (e.g. right part of L26151*a*, L26153), although a pathological cause cannot always be excluded (see e.g. the elevation on the fifth pleura of L26150*a*).

AFFINITIES

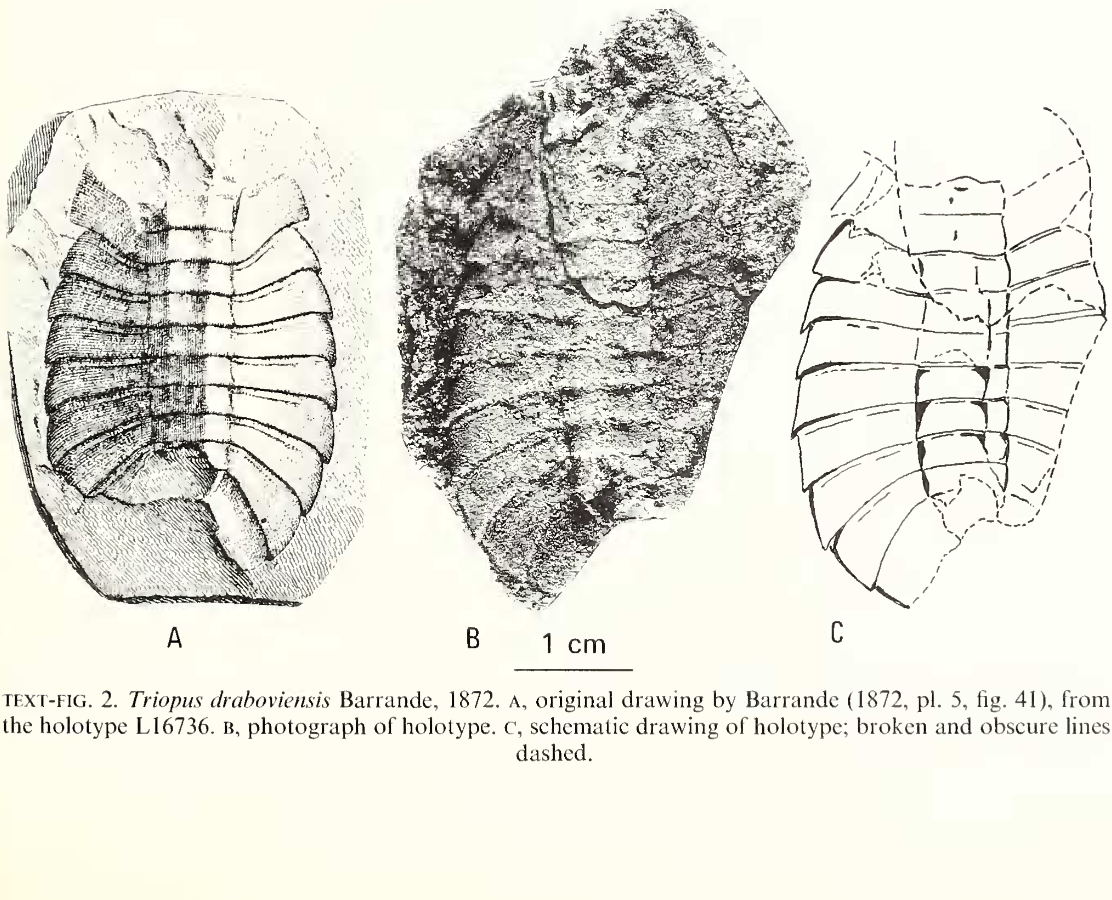
Duslia cannot be ranged with the polyplacophoran molluscs because it exhibits a different morphology of the cephalic shield (with differentiated glabellar region), a larger number (ten) of tergites with distinct trilobation and pronounced rhachis and pleurae, and because the posterior termination of the trunk differs markedly from all polyplacophorans. The spinose fringe along the dorsal exoskeleton may resemble the girdle of polyplacophorans, but its nature is quite different (spines are projections of individual dorsal segments of *Duslia*).

Duslia shows certain similarities to trilobites, and especially to the unusual non-trilobite arthropods *Triopus draboviensis* Barrande, *Cheloniellon calmani* Broili, and *Pseudarthron whittingtoni* Selden and White. *Duslia* shares with trilobites a marked longitudinal trilobation of the exoskeleton, the trilobite-like cephalic shield with its clearly differentiated glabellar region, and the configuration of rhachis and pleurae. The basic difference, however, is the absence of a pygidium, and the trunk being terminated by a telson with furcal rami. Other less important features differentiating *Duslia* from trilobites are the absence of facial sutures, the radial arrangement of trunk tergites and their firm connection along the sagittal axis, the inter-tergite boundaries maintaining their course at the dorsal furrows, and the uniform spinose fringe bordering the dorsal exoskeleton.

T. draboviensis Barrande, 1872 is based on a single specimen from Drabov (Děd) hill near Beroun. It may be from the same stratigraphical horizon as *Duslia* or be somewhat younger; it is preserved in a yellowish quartzite with fragments of *Dalmanitina socialis* (most common in the upper fossiliferous horizon of the Letná Formation, as distinguished by Chlupáč 1975). The holotype of *T. draboviensis*, L16736, newly recognized in the collections of the National Museum, Prague, represents an incomplete trunk showing nine radially arranged tergites with a rhachis differentiated by shallow and ill-defined dorsal furrows. Pleurae are smooth, slightly overlapping, and widen markedly abaxially; their posterolateral extremities are sharp, each being produced into a short spine. Pleural furrows are only faintly indicated near the anterior margin of some pleurae. The most posterior (left) pleura preserved extends behind the end of the rhachis in a manner that leaves no place for a pygidium, and a spine-like telson may be postulated. Pleural regions are inclined steeply abaxially.

The one specimen of *Triopus* is preserved as an internal mould, compacted in a longitudinal direction. Anteriorly it is obscured by weathering and the coarseness of the sediment to such an extent that it is unclear whether the most anterior portion represents the posterior part of the cephalic shield or a remnant of a trunk tergite. Longitudinal depressions on the rhachis close to the dorsal furrows are irregular and evidently caused (or at least accentuated) by secondary deformation. In this respect, and also in the right extremities of pleurae, Barrande's original figure (1872, pl. 5, fig. 41) is idealized and restored (cf. text-fig. 2 herein).

Although *Triopus* resembles *Duslia* in its trilobation and gross morphology of radially arranged tergites, it differs markedly in convexity of the exoskeleton, the different proportions of the rhachis and pleurae, and the absence of a spinose fringe. The supposed cephalic shield of *Triopus* (*Zonozoe* or *Drabovaspis*; Chlupáč 1965; Bergström 1968) exhibits a completely different morphology to that of *Duslia*.



TEXT-FIG. 2. *Triopus draboviensis* Barrande, 1872. A, original drawing by Barrande (1872, pl. 5, fig. 41), from the holotype L16736. B, photograph of holotype. C, schematic drawing of holotype; broken and obscure lines dashed.

The systematic position of *Triopus* is uncertain. Barrande (1872) regarded it as a trilobite, Novák (1885) reassigned it to non-trilobite arthropods, while Jahn (1893) ranged it with the chitonids. Chlupáč (1965) stressed its similarity to aglaspids and combined it tentatively with prosomas described as *Zonozoe* Barrande or *Drabovaspis* Chlupáč. Bergström (1968) considered *Triopus* to be the trunk of *Drabovaspis* and referred it to xiphosurids. Although it is clearly non-trilobite and possibly xiphosuran (according to the less distinct trilobation, the radial arrangement of abaxially widened pleurae, and the evident absence of pygidium), its affinities remain obscure (especially because of its indifferent preservation).

C. calmani Broili, 1932 from the Lower Devonian (lower Emsian) Hunsrück Shale of Germany resembles *Duslia* in its oval outline, distinct trilobation, radial arrangement of tergites, shallow and indistinct axial furrows, flat pleurae, and possession of a telson and furcal rami. The cephalic shield of *Cheloniellon*, however, is markedly smaller and sagittally shorter, the eyes are well developed, the posterior pleurae widen considerably, and the furcal rami are notably prolonged (details in Stürmer and Bergström 1978). No spinose fringe, so characteristic of *Duslia*, is present in *Cheloniellon*.

Cheloniellon is the only arthropod comparable with *Duslia* in which appendages have been preserved, but even this feature fails to conclusively resolve its systematic position. Broili (1932, 1933) referred *Cheloniellon* to a separate subclass of Crustacea, Størmer (1959) assigned it to the subclass Trilobitoidea of the Trilobitomorpha (which appears to be a heterogeneous group; Whittington 1979; Briggs 1983), while Stürmer and Bergström (1978) concluded that it occupies a position intermediate between trilobitomorphs and chelicerates (cf. also Bergström 1979, 1980).

The small Upper Silurian *P. whittingtoni* Selden and White, 1984, from the Ludlovian lagoonal deposits of Scotland, resembles *Duslia* in its oval outline, distinct trilobation, and gently radiating flat pleurae. The incompletely preserved cephalic shield, however, was evidently much smaller than in *Duslia*, with the number of trunk tergites being only seven or eight, the rhachis broader, and the pleural furrows sharper. The exoskeleton of *Pseudarthron* does not show the fringe which is so typical of *Duslia*. The systematic position and affinities of *Pseudarthron* are uncertain, although its non-trilobite nature is clear.

As the appendages of *Duslia* are unknown, its systematic position and affinities remain doubtful. The morphology of the dorsal exoskeleton points to Trilobitomorpha but not to the class Trilobita proper. The systematic position of *Duslia* may be analogous to that of *Cheloniellon*.

ENVIRONMENT AND PALAEOECOLOGY

Duslia occurs in marine deposits characterized by an alternation of lighter grey (yellow and brown if weathered) sandstones and subgreywackes with markedly darker sandy and clayey siltstones in beds several centimetres to several tens of centimetres thick. Sandstone beds (locally quartzites) show frequent sedimentary and biogenic structures on bedding planes, and the siltstones commonly exhibit traces of bioturbation. Most fossils are concentrated in thicker sandstone layers with organic debris and siltstone and claystone pebbles. Graded bedding is infrequent and the siltstones are laminated in some layers. According to Kukal (1958, 1963), the lithology suggests shallow water, nearshore sedimentation within the reach of river-borne material, and a periodically changing climate (possibly seasonal fluctuations).

Both *Duslia*-bearing localities, Ostrý hill and Veselá, have been well-known palaeontological localities since Barrande's time. Sandstone slabs with *Duslia* contain scattered, disarticulated remnants of trilobites *Deanaspis goldfussi* (Barrande) and *Dalmanitina socialis* (Barrande), ostracods, sporadic *Metaconularia anomala* (Barrande), and rare orthoconic nautiloids. At both localities, some sandstone layers are rich in fragmented trilobites: apart from the dominant *Deanaspis goldfussi* and *Dalmanitina socialis*, less common forms include *Selenopeltis buchi* (Barrande), *Opsimasaphus ingens* (Barrande), *Pharostoma pulchrum mendax* Vaněk, *Zelizskella hawlei* (Barrande), *Eccoptochile clavigera* (Beyrich), *Stenopareia panderi* (Barrande), and *Primaspis primordialis* (Barrande). Associated with these trilobites are orthid brachiopods *Drabovia redux* (Barrande), *Draboviuella draboviensis* (Barrande), and the less common *Petrocrania obsoleta* (Barrande), gastropods, bivalves, conulariids, and nautiloids, while echinoderm debris occurs in some layers. Ichnofossils commonly include the vertical and oblique burrows *Monocraterion*, *Skolithos*, *Arenicolites*, and *Diplocraterion*, rarely the fasciculate *Phycodes*, and very frequently the epistratal *Palaeophycus*, *Gordia*, and (ubiquitous) *Planolites*.

The composition and preservation of the fauna indicates a shallow water and high energy *Benthic Assemblage 3* in Boucot's (1975) classification, and the same is postulated from the ichnofossils ranged within the *Cruziana* Ichnofacies (cf. Chlupáč 1965; Havlíček 1982; Chlupáč and Kukal, in press).

The occurrence of *Duslia* as complete and articulated exoskeletons contrasts strikingly with the fragmentary preservation of associated fossils and deserves particular attention. Complete trilobite exoskeletons have been recovered from sandstones at Veselá, but they are very rare.

The fourteen specimens of *Duslia* (some with counterparts) collected at Veselá at the turn of the nineteenth century (originally housed at the Technical universities in Prague and Brno, but now in the National Museum and Geological Survey, Prague) all most likely derive from the same layer of light grey, impure sandstone, 60–90 mm thick. This is evidenced not only by lithology but also by analogous lower and upper bedding planes of the *Duslia*-bearing slabs of rocks. The relative position of the *Duslia* exoskeletons seems to be uniform, with the dorsal side turned towards the flatter bedding plane, and the same position is confirmed by pairs of specimens preserved in close proximity on the same slab of rock (L26149*a*, *b*, L26150*a*, *b*, L26157*a*, *b*, L26160*a*, *b*, ICh522*a*, *b*). Due to a lack of primary documentation during collection it is not clear whether the specimens were deposited dorsal side upwards or downwards. All known specimens of *Duslia* lie within the sandstone layers and none was found directly on the bedding plane proper. Although freshly killed soft-bodied arthropods can survive turbulent transport over substantial distances, as recently shown by Allison (1986) under experimental conditions, the exclusive preservation of complete exoskeletons of *Duslia* and their uniform position within the sandy layers suggest that the specimens were not subjected to any significant transport and are preserved in life position.

The firm connection of exoskeletal elements in the axial part suggests that *Duslia* was incapable of enrolment. The most characteristic feature of *Duslia*—the spinose fringe bordering the whole exoskeleton—may have protected limbs or other soft parts in the sandy environment. The thin carapace of *Duslia* was evidently not suitable for a high energy environment on the substrate itself and, in view of its broadly oval shape and flat morphology, the absence of eyes, and other features mentioned above, I conclude that *Duslia* lived buried in the unconsolidated sandy substrate close to the sediment–water interface.

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